

FINAL REPORT

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**CENTRIFUGE EXPERIMENTS ON VESTIBULAR CORIOLIS AND
Lz NYSTAGMUS**

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HUMAN VESTIBULO-OCULAR RESPONSE DURING 3 G_Z CENTRIFUGE STIMULATION.

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Abstract — The vestibulo-ocular reflex (VOR) and spatial orientation perceptions were recorded in 15 subjects during a 3 G_Z centrifuge run. These data were obtained to study two issues; first, to gain insight into reports of asymmetrical disorientation and disturbance during acceleration and deceleration of G-induced loss of consciousness (G-LOC) training centrifuges. Second, to study the effects of sustained vertical linear acceleration on the vestibular system. The centrifuge run consisted of an acceleration to 3 G_Z in 19 s, sustained 3 G_Z for 5 min, and a deceleration to 1 G_Z in 19 s. The runs were repeated three times with the subject facing the motion, and three times with the subject's back to the motion. The VOR and spatial orientation perceptions from the eight subjects who completed all six runs were analyzed. The total VOR response during acceleration and deceleration of a centrifuge run is composed of interacting angular and linear VOR components. However, the VOR response did not correspond to reported asymmetries in pitch orientation perception between centrifuge acceleration and deceleration. During the constant velocity high G phase of a centrifuge run, a sustained up-beating ("L_Z") nystagmus was

observed in 14 of the 15 subjects. For the eight subjects analyzed, L_Z nystagmus was shown to be an individual subject characteristic, and displayed a range of mean magnitudes from 0 to 10 deg/s at 90 s. Assuming a normal visual suppression ratio of the VOR, the magnitudes of the L_Z nystagmus in our subject sample did not appear sufficient to degrade visual acuity.

Introduction

Centrifuges are employed in aerospace medicine to train military pilots to counter G-LOC, and are being considered as a means of providing familiarization with some aspects of spatial disorientation. During centrifuge acceleration and deceleration, the cabin is rolled so that the resultant gravito-inertial force remains directed downward along the subject's Z-body axis. However, rolling the subject's Z-body axis away from the axis of centrifuge rotation produces a Coriolis stimulus to the semicircular canals. As a result, subjects experience illusory sensations of pitch, roll, and yaw that differ considerably from the sensations generated by an aircraft in pulling out of a coordinated bank-and-turn at comparable G levels.

Decelerations from centrifuge runs are nauseogenic and induce an immediate disorientation stress reaction in many subjects (1). Our study was encouraged

by Houghton, who, recalling the disturbance he had experienced during deceleration on a 50 ft radius centrifuge in a G-LOC experiment (2), discussed with us the feasibility of a 300 ft radius centrifuge for G-LOC avoidance training. However, it is interesting to note that deceleration from a 9 G run on a 300 ft radius centrifuge will still generate a perceived forward pitch tumble of about 56 deg/s that would be completely different from the flight experience, and probably disturbing to a number of subjects. Understanding the mechanisms of this undesirable reaction to centrifuge deceleration is an important step in improving aviator acceptance of GLOC training. Of greater importance is the development of the ability to predict reactions to many combinations of linear and angular accelerations that occur in every day life, and in various maneuvers of aerospace vehicles. A number of experiments have indicated that subtle differences in combinations of linear and angular accelerations alter several aspects of vestibular reactions, perhaps differentially, and that G level and change in magnitude and direction of G are significant factors in immediate disorientation stress, motion sickness, and sensorimotor aspects of the overall reaction (3 - 5).

Mathematical models for the human angular VOR can be used to predict the response for any centrifuge profile. Figure 1 shows the predicted time course of horizontal and vertical slow phase velocity (SPV) for a 3 G_z pendulous centrifuge profile, such as the one used in our experiments. The initial response is a horizontal eye movement. However, as the subject's Z axis rolls 70.5 deg, the horizontal canal stimulus decreases, and the vertical canals enter the plane of rotation. A prominent vertical nystagmus crescendo and decay, followed by a slight response reversal (due to the model "adaptation" term) is predicted over the following minute. The model, which considers only the angular acceleration stimulus to the semicircular canals, predicts that nystagmus disappears by the time the centrifuge begins to decelerate.

As the centrifuge decelerates, the horizontal canals rotate quickly back into the plane of rotation. The model predicts a transient right beating, then left beating nystagmus as the centrifuge slows, and a down-beating vertical nystagmus crescendo, decay, and slight adaptation reversal soon after the centrifuge has halted. The predicted magnitude of the vertical SPV response during centrifuge acceleration and deceleration are similar, though opposite in direction. This model also predicts that SPV responses from a subject seated with his back to the motion, which was one of the conditions in our experiment, should be equal and opposite to that shown in Figure 1.

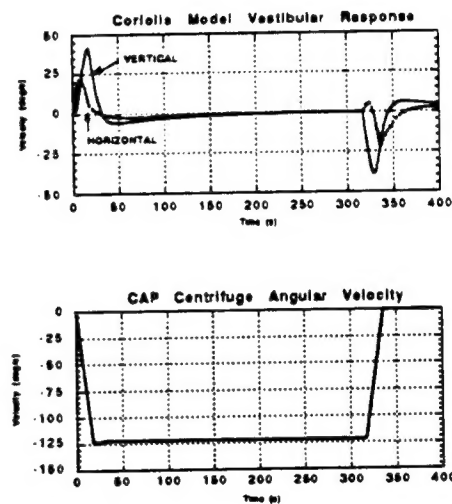


Figure 1. CAP centrifuge angular velocity stimulus and predicted Coriolis model horizontal and vertical slow phase velocity.

[Note: The model used assumed a head angular velocity to slow phase velocity transfer function of a form:

$$\frac{SPV(s)}{\omega(s)} = \frac{Ks^2(\tau_i s + 1)}{(\tau_c s + 1)(\tau_a s + 1)(\tau_v s + 1)}$$

where τ_c = semicircular canal cupula time constant, 6 seconds.

τ_a = adaptation time constant, 80 seconds.

τ_i and τ_v = are central velocity storage parameters, 7.5 s and 15 s for horizontal response, respectively, and 2.7 s and 5 s for vertical responses, respectively.

K = system gain, 144 for horizontal responses and 88 for vertical

responses, corresponding to a high frequency VOR gain of 0.6.

The primary afferent response from the semicircular canal is thought to be independent of G level, but different aspects of the total reaction to semicircular canal stimulation, including the VOR, are influenced by changes in magnitude and direction of the G vector. The apparent time constant of post rotatory nystagmus is altered when the head and body are tilted relative to gravity (6), possibly because central angular velocity storage mechanisms are G dependent (7). Horizontal nystagmus is generated by sinusoidal change in horizontal linear acceleration along the intra-aural (y-axis) of the head (8). Young (9) postulated the existence of an additive "L" nystagmus component due to linear acceleration. Using data from Lansberg, Guedry and Graybiel (10) and other studies, Young estimated the magnitude of the L nystagmus component to be in the range between 5-18 deg/s/G. Young noted that the time course of L nystagmus response to gravito-inertial acceleration exhibited nonlinear dynamics characteristics. Marcus (11) and Marcus and Van Holten, (12) exposed five subjects to a 3 G_z stimulus for 3 min on a pendulous centrifuge, and found an up-beating nystagmus. Analyzing their electro-oculography (EOG) records of vertical eye position using Young's method (9), they estimated the vertical L_z nystagmus component to be 27 deg/s at 16 s from G onset, and 11 deg/s after 3 min. They noted that such a nystagmus might negatively impact an aviator's vision during high G maneuvers.

In preliminary centrifuge runs for this study, eye movements recorded by EOG suggested major idiosyncratic differences in the magnitude of L_z nystagmus; one individual having magnitudes seemingly sufficient to blur vision during high G maneuvers. However, the apparent high magnitude of the L_z nystagmus may have been more artifact due to EOG rather than a physiological response. The relationship between vertical eye displacement and EOG potential is

nonlinear (13), and drift in EOG offset potential makes vertical eye displacement, and hence eye velocity difficult to accurately estimate using EOG. Dynamic EOG artifacts due to lid motion are also present (14).

This study will address several issues concerning the vestibulo-ocular response during two phases of a centrifuge run: First, during centrifuge acceleration and deceleration, how well does the observed VOR follow the predictive model, and will the anecdotally reported acceleration/deceleration differences in perceived spatial orientation dynamics be present when the centrifuge angular acceleration and deceleration magnitudes are low? Can perceptual counterparts of the total reaction be inferred from the VOR?

Secondly, during the sustained hyper-G portion, does a linear L_z nystagmus exist and what are the range of magnitudes? Are substantial individual differences in L_z nystagmus present in recordings made by a procedure that avoids EOG artifacts, and are such differences sustained over several repeat test sessions?

Method

Fifteen U.S. Navy and Marine aviator candidates who were awaiting flight training served as subjects. The subjects were male, aged 21-24 years old. All had passed Navy flight physical examinations without evidence of vestibular disorders. None of the subjects had experienced sustained hyper-G, either in a centrifuge or high performance aircraft, prior to the experiment.

The Coriolis Acceleration Platform (CAP; 15) was used to create the 3 G_z stimulus shown in Figure 1. A gimballed chair in a darkened cabin located 20.5 ft from the centrifuge rotation axis was installed on the CAP. Subjects sat head erect in the chair, which was free to roll about an earth horizontal axis through the subject's chest and tangential to the

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rotation path. The centrifuge profile for each run consisted of a constant angular acceleration for 19 s to a constant velocity of 122 deg/s. This created a 3 G_z force (eyeballs down) on the subject that was sustained for 5 min. A constant deceleration for 19 s completed the run. Three runs were made with the subject facing the direction of motion (clockwise rotation), and three runs were made with the subjects back to the motion (counterclockwise rotation). One run was made per day to avoid fatigue effects. As shown in Table 1, the run direction order was randomized to avoid habituation effects. Eight subjects completed all six runs, typically over 8 or 9 days. Only their data were analyzed for this study. Six others experienced G-LOC during one or more runs, which were immediately terminated. One subject became ill for unrelated reasons and withdrew from the study.

Table 1: Run Order

Subject	Run						
	#1	#2	#3	#4	#5	#6	#7
s1	CW	CCW*					
s2	CCW	CW	CCW	CW	CCW	CW	
s3	CW	CW	CW	CCW	CCW	CCW	
s4	CCW*						
s5	CW	CCW	CW	CCW	CW	CCW	
s6	CW	CCW	CW	CCW*	CCW	CW	CCW
				*			
s7	CW	CCW	CW	CCW	CW	CCW	
s8	CW	CCW	CW	CCW	CW	CCW	
s9	CCW*						
s10	CW*						
s11	CW	CCW	CW	CCW	CW	CCW	
s12	CW*	CW*					
s13	CCW	CW	CCW	CW	CCW		
s14	CW	CCW	CW	CCW	CW*	CCW	CW
s15	CW	CCW	CCW	CW	CCW	CW	

* GLOC episode

** CAP Mechanical Failure, no data.

An adjustable occipital head cup was used to position and stabilize the head. Before each run, the subject's head was positioned such that the plane described by the line between the outer canthus of the eye and the top of the tragus was approximately 20 deg above the earth horizontal. The subject was instructed not to move his head throughout the run. However, if GLOC occurred, the head was free to drop forward, restoring blood

flow to the brain. Mental arithmetic, general knowledge, and sensation questions were asked throughout the run to maintain alertness and monitor subject safety. Subjects answered yes or no to the questions using key presses.

Subjects were instructed to gaze "straight ahead" for the duration of the centrifuge run. Movements of the subject's right eye were recorded in darkness using a head mounted infrared video-oculography system. The system consisted of a headband mounted video camera (Pulnix TM-540), which imaged the eye from above using a dichroic mirror and LED infrared light sources. To ensure that there was no relative motion between the camera and the eye, the helmet was equipped with a bite-bar. The video signal of the eye was processed by a device (ISCAN, Inc., Cambridge MA, Model RK-426 Pupil/Corneal Reflection Tracking Unit) designed to track pupil movement in real time at a sampling rate of 60 Hz. The ISCAN processor was normally calibrated using +/- 10 deg horizontal and vertical targets, mounted at a distance of 54 inches. In a separate study, the linearity of the ISCAN system calibration characteristic was confirmed over a +/- 30 deg range (16).

Subjects were interviewed immediately after each run, using a standard list of questions. They were asked to describe the changes in perceived orientation they had experienced during the run, and to reproduce them using a small hand held mannequin.

Horizontal and vertical eye position data were transferred to a Macintosh computer for further analysis. Fast phases were detected, and SPV were estimated using a single axis, single pass, acceleration based algorithm (17). Slow phase velocity down (up-beating nystagmus) was defined as positive, and SPV to the left (right beating nystagmus) was defined as positive (18). Missed fast phases were then removed manually. Calculation of calibration scale factor,

manual editing, filtering, decimation, and statistical analysis were performed using MatLab (MathWorks, Inc.).

acceleration, regardless of the direction of centrifuge rotation.

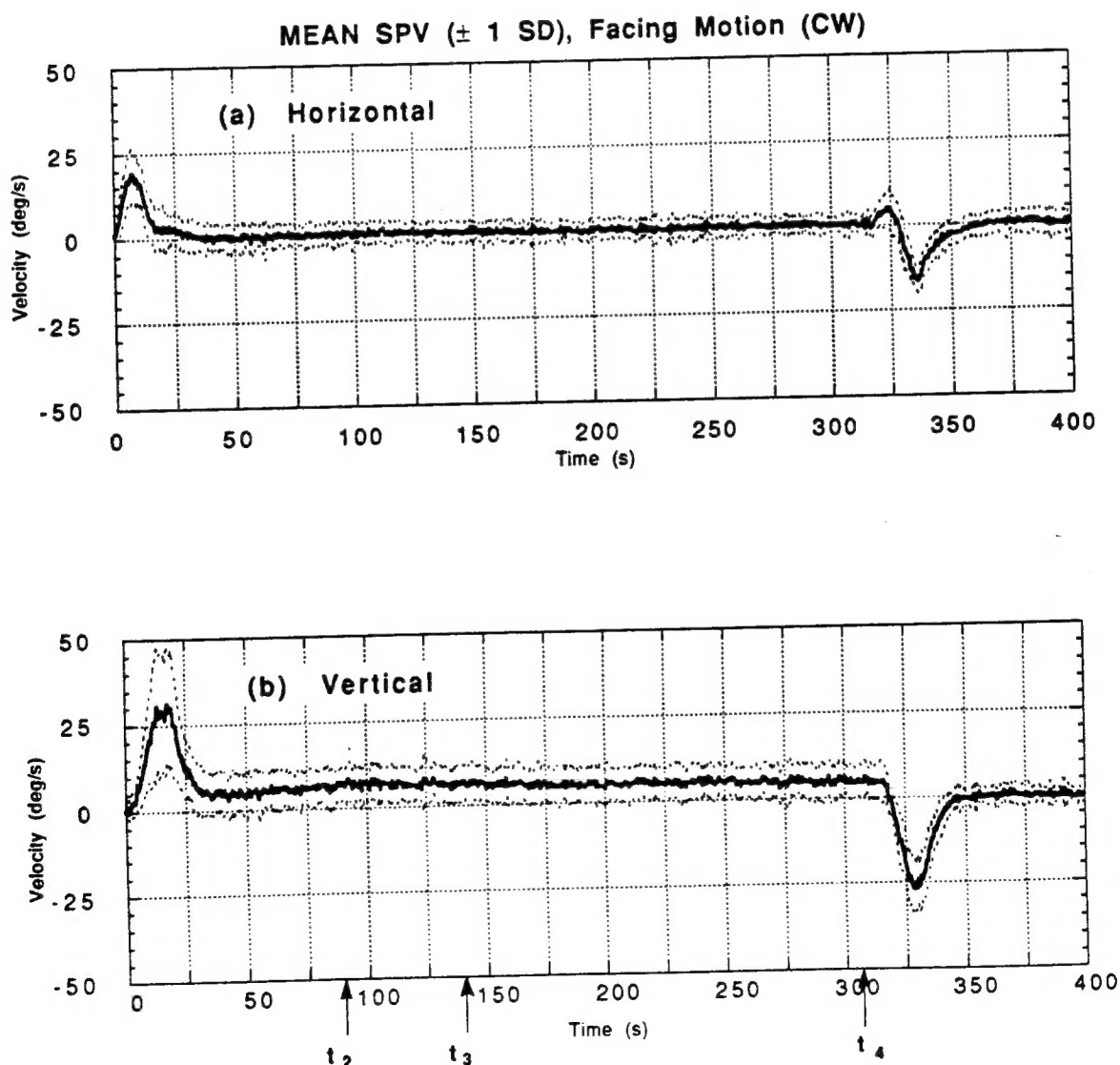
Slow Phase Velocity Response

Results

Sensations

Guedry, Rupert, McGrath and Oman (19) provide a full description of the perceived changes in spatial orientation for this centrifuge experiment. In summary, subjects indicated that perceived pitch change was consistently greater during deceleration than

Figure 2 shows the mean horizontal and vertical SPV responses obtained for the eight subjects who completed all six runs. Figures 2a and 2b show mean responses for forward facing CW runs, and Figures 2c and 2d show mean SPV responses for back to motion CCW runs. Also, L_z nystagmus was observed in all 7 subjects who did not complete all six runs, so that 14 of the 15 showed an L_z nystagmus during a 3 G_z centrifuge run.



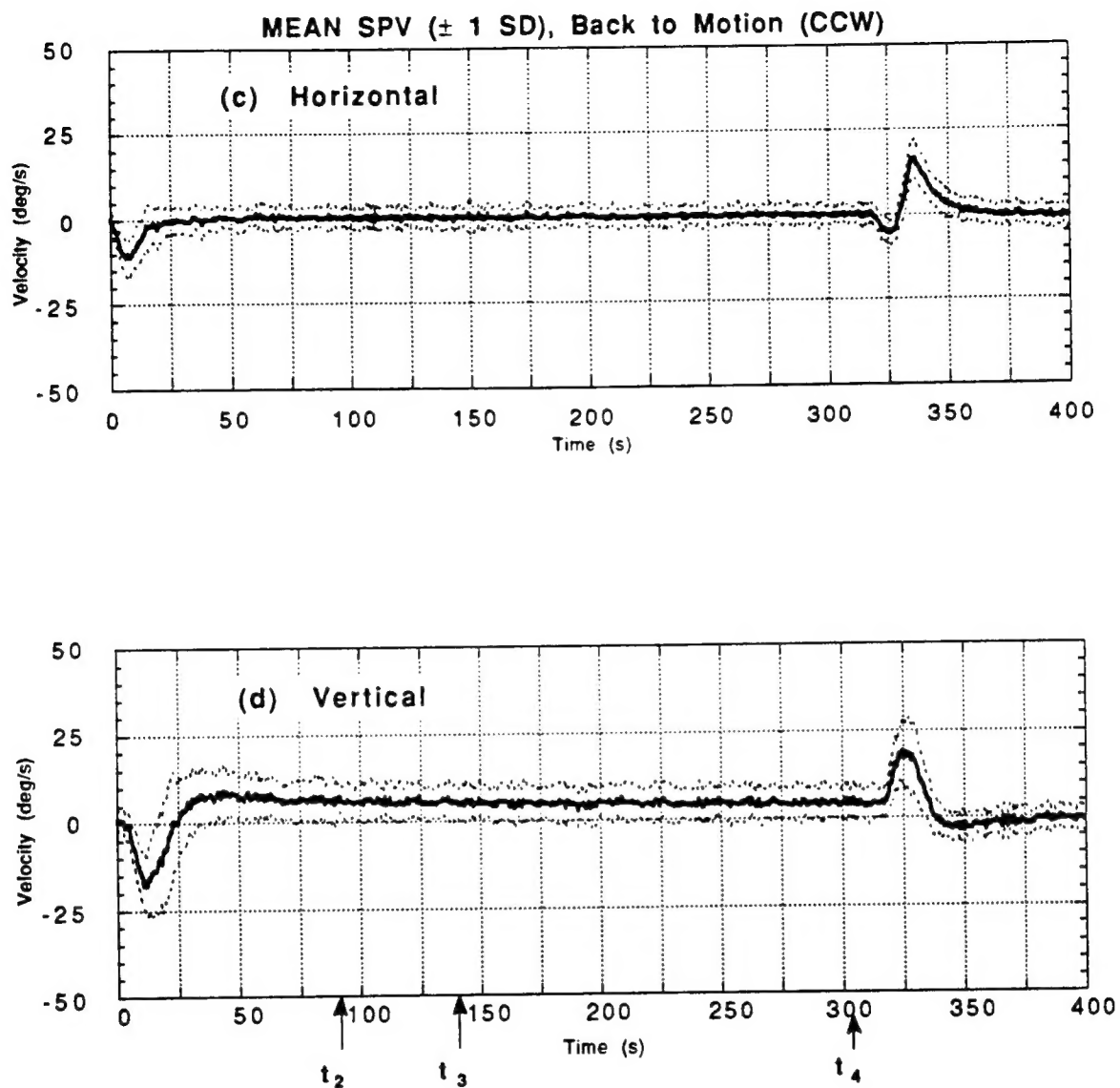


Figure 2. (a) Mean horizontal SPV for facing the motion (CW) runs.
 (b) Mean vertical SPV for facing the motion (CW) runs.
 (c) Mean horizontal SPV for back to the motion (CCW) runs.
 (d) Mean vertical SPV for back to the motion (CCW) runs.

[Note: For presentation of means the original 60 Hz SPV data file was decimated to 5 Hz after lowpass filtering the data with an 8th order Chebyshev type I filter with cutoff frequency 2 Hz. The 5 Hz SPV data file is then further lowpass filtered with a 12th order Chebyshev type I filter with cutoff frequency 1 Hz. For both low pass filters, the input sequence is filtered in both directions to remove all phase distortion.]

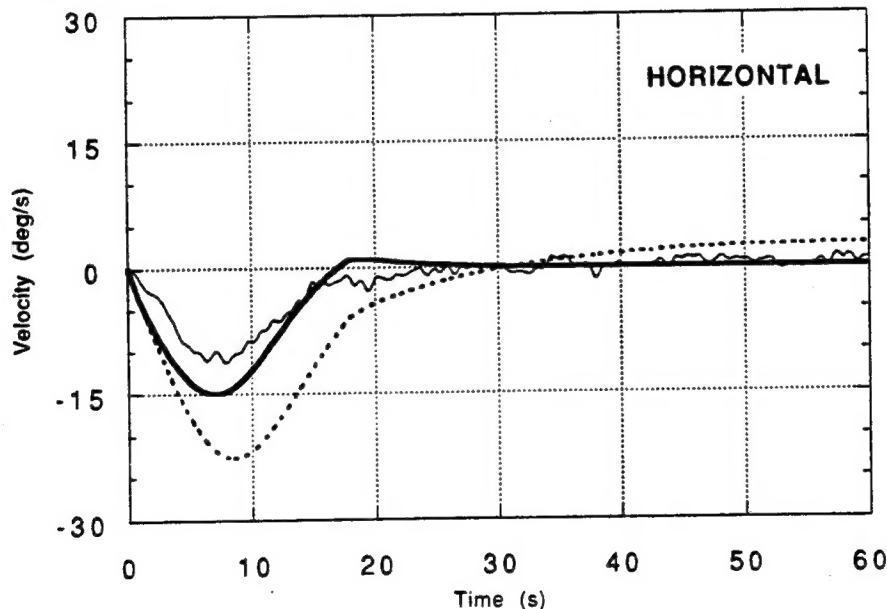
Slow Phase Velocity Response

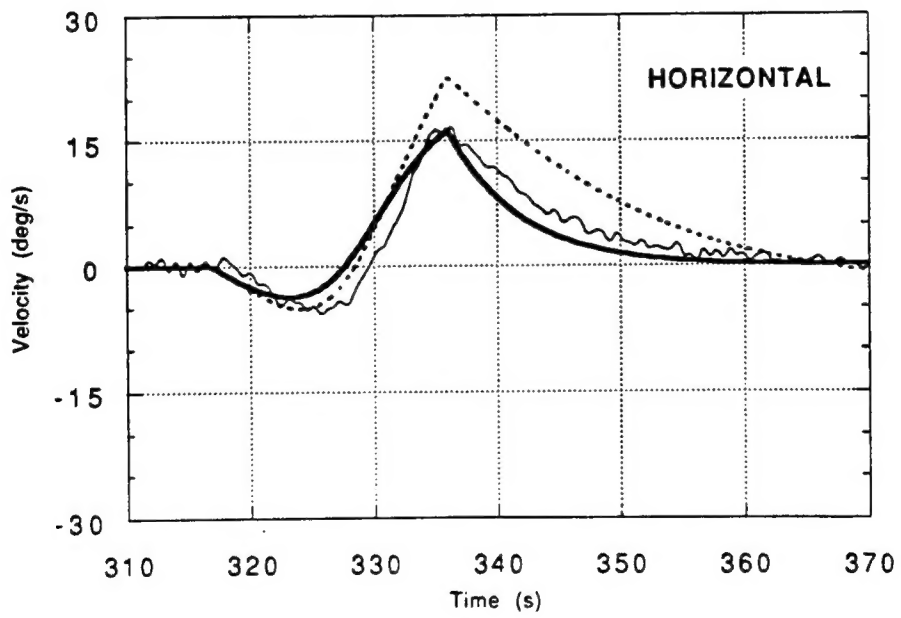
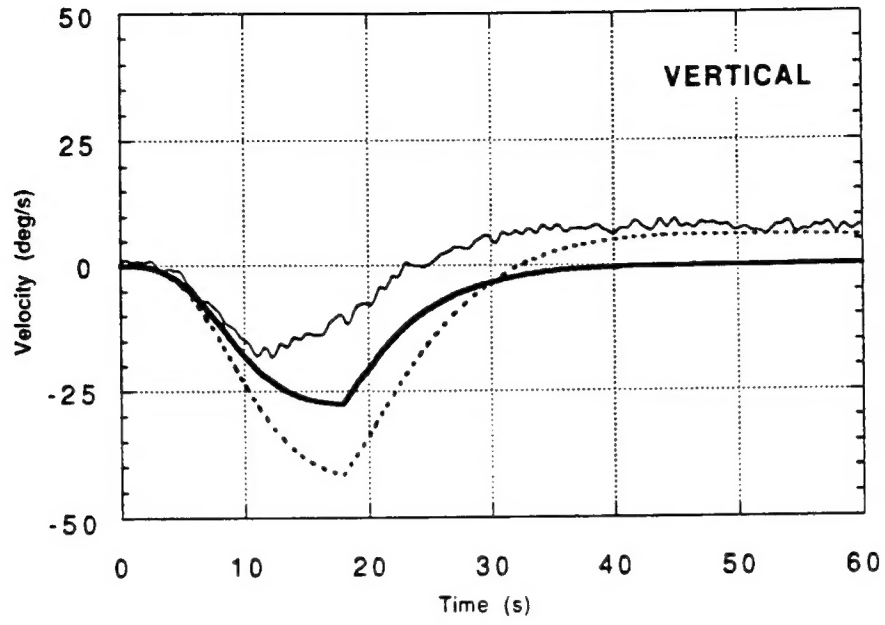
Figure 2 shows the mean horizontal and vertical SPV responses obtained for the eight subjects who completed all six runs. Figures 2a and 2b show mean responses for forward facing CW runs, and Figures 2c and 2d show mean SPV responses for back to motion CCW runs. Also, L_z nystagmus was observed in all 7 subjects who did not complete all six runs, so that 14 of the 15 showed an L_z nystagmus during a $3 G_z$ centrifuge run.

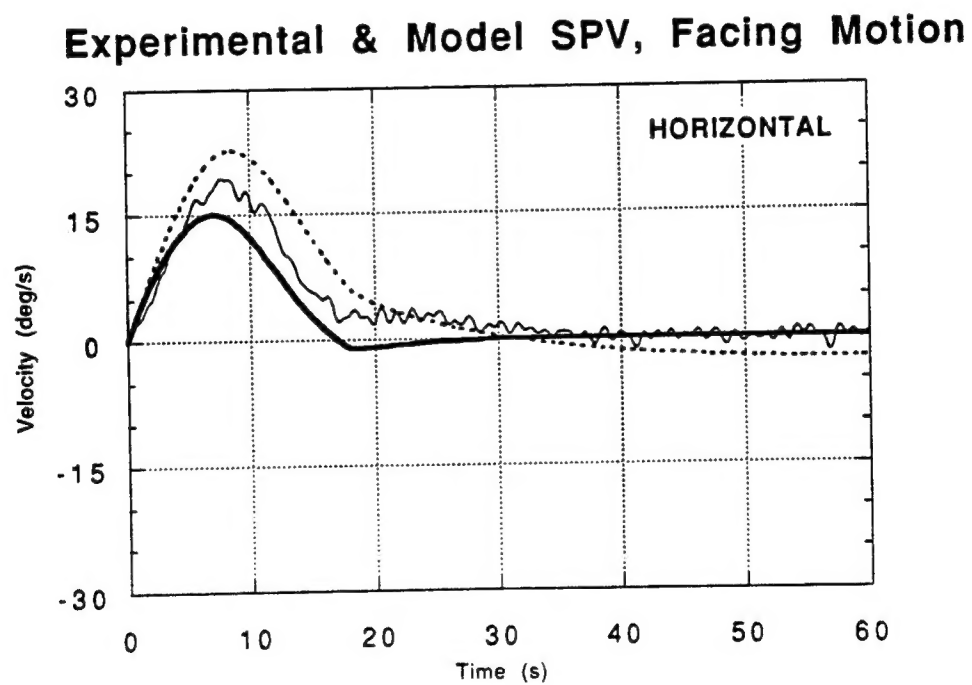
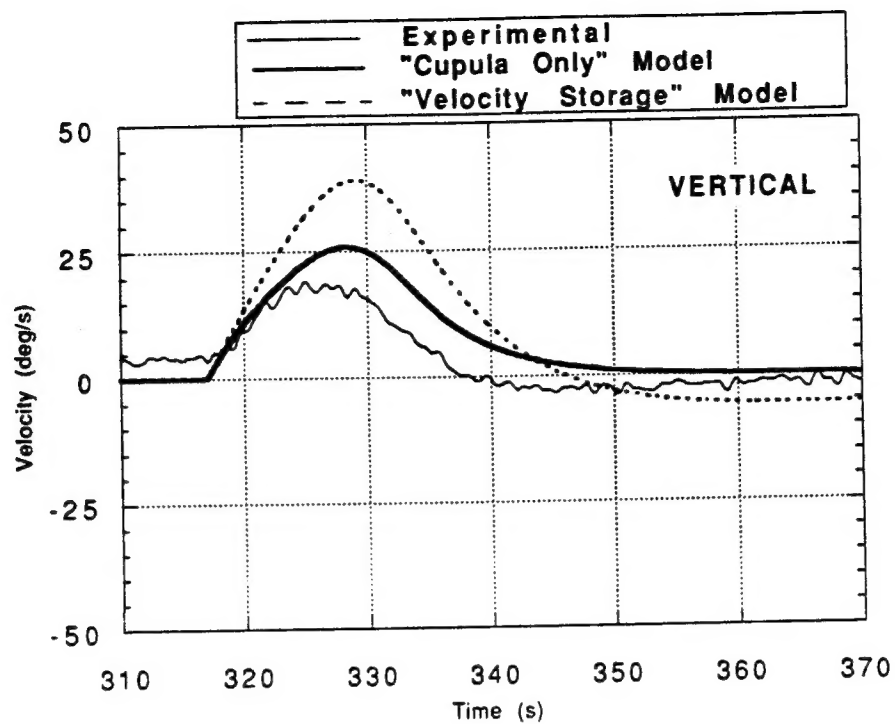
Figure 3 shows the experimental SPV and the predicted SPV from the "velocity storage" model presented in Figure 1 during the period of the angular SPV response, that is, during the 19 s of angular acceleration of the centrifuge and for approximately 40 seconds thereafter.

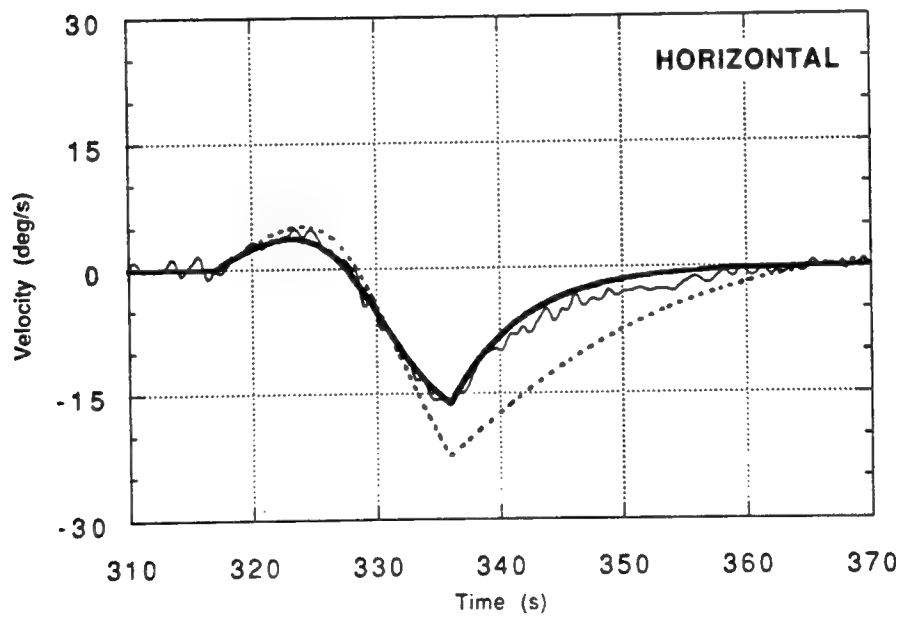
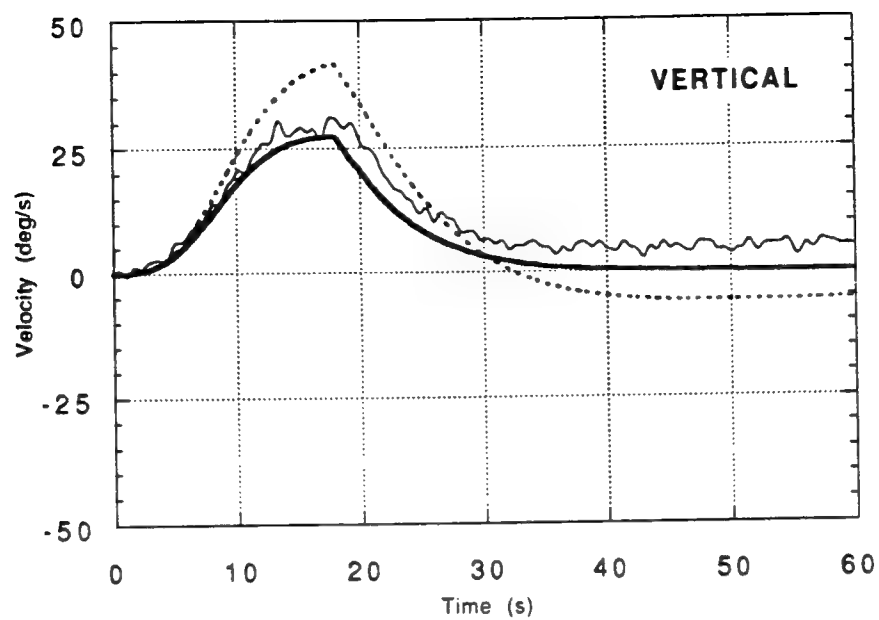
In general, the experimental response followed the predicted response fairly well with several notable exceptions: 1) the vertical eye velocity did not return to the predicted baseline during constant angular velocity; 2) the gain of the vertical response was far below the predicted gain of 0.6; 3) the gain of the horizontal response was below the predicted gain of 0.6; 4) Following deceleration, the vertical response did not overshoot the baseline as predicted. To investigate these discrepancies, we added the predicted SPV from a "cupula only" model without velocity storage and adaptation effects to Figure 3. For both horizontal and vertical SPV, this cupula model response provides a qualitatively better fit to the experimental response than the velocity storage model.

Experimental & Model SPV, Back to Motion









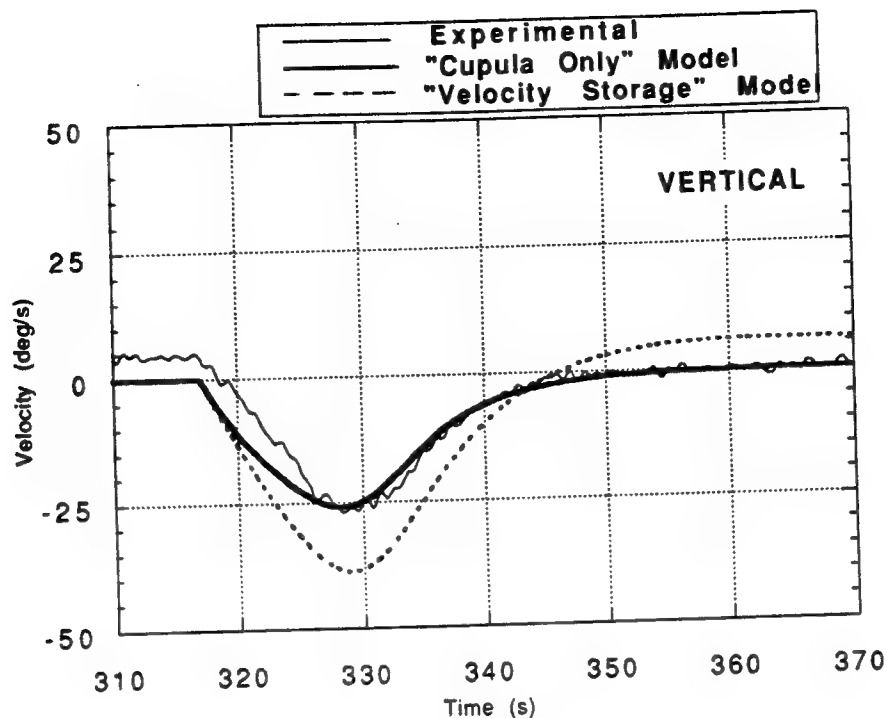


Figure 3. Mean experimental, predicted velocity storage model, and predicted cupula model horizontal and vertical SPV for facing the motion (CW), and back to the motion (CCW) runs.

To calculate the mean experimental SPV response, data from subjects that experienced GLOC were excluded, and data from a subject's first run were excluded. The responses from run one were excluded because the magnitude of the peak SPV during centrifuge acceleration for a subject's first run differed from subsequent runs (see Tables 2 and 3). Statistical analysis on data from subjects who completed a CW run first showed that the difference in vertical SPV magnitude during CW acceleration between runs 1 and the average of runs 2 and 3 was significant ($F = 16.74, p < 0.01$). Subject s2 was the only subject who completed a CCW run first. The first run response of s2 was different than responses from subsequent runs. In run 1, the vertical SPV magnitude during acceleration has a value of -7 deg/s, as compared with -12 deg/s and -10 deg/s for subsequent CCW runs. Our data indicate a significant order effect that is consistent with literature

pointing to augmented vestibular responses during first exposure and/or experimentally induced arousal (20).

The overall shape of the SPV responses was similar for all runs in a given direction (Figures 2 and 3). However, there were individual differences in the peak SPV magnitudes and in response decay during the constant velocity phase of the stimulus profile. Tables 2 and 3 present SPV values for each of the eight subjects at different points in the time course of the response to centrifuge runs. Data from forward facing and backward facing runs are presented in Tables 2 and 3, respectively. The subscript numbers used in Tables 2 and 3 correspond to the following specific times:

- 1 - time of maximum SPV during acceleration
- 2 - 90 s
- 3 - 140 s
- 4 - 305 s

5 - time of horizontal SPV

"reversal"

6 - time of maximum SPV during deceleration.

For example, t_{6H} is the time of maximum horizontal SPV during deceleration, and V_2 is the vertical SPV at time $t = 90$ s.

Run	Horizontal						Vertical						
	t_{1H}	H_1	t_{5H}	H_5	t_{6H}	H_6	t_{1V}	V_1	V_2	V_3	V_4	t_{6V}	V_6
s2-2	8	31	323	4	334	-22	15	63	10	9	6	329	-23
s2-4	8	22	322	3	334	-22	16	57	8	6	4	331	-30
s3-1	10	25	324	11	338	-9	20	51	6	8	2	328	-37
s3-2	9	33	326	10	336	-16	15	45	7	5	2	327	-40
s3-3	9	32	325	16	336	-13	16	40	6	5	3	329	-39
s5-1	10	19					19	63					
s5-3	9	21	326	11	335	-13	17	51	14	12	11	329	-30
s5-5	8	20	324	7	335	-12	19	54	8	8	7	330	-32
s6-1	9	18	323	5	334	-12	19	34	15	12	12	324	-35
s6-3	9	21	324	5	335	-15	18	29	12	12	8	328	-25
s6-6	10	16	325	3	335	-15	19	30	10	10	9	328	-16
s7-1	11	24	326	4	336	-17	18	41	6	6	5	329	-26
s7-3	11	22	325	6	336	-16	18	30	5	5	5	328	-23
s7-5	11	26	323	8	335	-17	19	30	7	8	8	327	-29
s8-1	8	14	325	8	337	-17	20	36	13	13	8	331	-28
s8-3	9	13	325	9	336	-17	19	24	8	9	7	330	-30
s8-5	8	18	324	5	336	-15	18	24	9	9	8	331	-27
s11-1	9	12	325	3	335	-17	20	21	3	2	2	328	-19
s11-3	9	11	325	3	335	-19	18	14	2	1	1	326	-25
s11-5	7	16	326	6	336	-19	16	16	3	1	1	327	-25
s15-1	12	16	324	3	337	-23	19	19	0	0	0	332	-49
s15-4	9	13	323	0	336	-22	16	12	-1	-2	-1	331	-36
s15-6	12	15	323	0	336	-31	19	14	0	0	0	330	-31

Table 2: Facing the Motion Runs (Clockwise)

Run	Horizontal						Vertical						
	t_{1H}	H_1	t_{5H}	H_5	t_{6H}	H_6	t_{1V}	V_1	V_2	V_3	V_4	t_{6V}	V_6
s2-1	7	-14	323	-7	335	19	11	-7	21	19	11	327	27
s2-3	7	-17	323	-6	336	16	10	-12	11	8	3	325	21
s2-5	7	-16	327	-6	337	18	12	-10	10	7	3	328	24
s3-4	7	-13	324	-6	335	19	10	-20	7	5	2	330	26
s3-5	7	-16	325	-3	336	23	10	-24	4	4	2	327	33
s3-6	6	-18	325	-7	335	25	10	-26	7	6	3	328	29
s5-2	9	-12	326	-13	337	20	12	-17	14	12	12	328	42
s5-4	10	-15	328	-11	336	13	13	-17	9	7	7	327	34
s5-6	6	-18	323	-12	335	21	10	-16	7	7	6	328	35
s6-2	6	-7	325	-5	336	18	12	-10	10	9	8	326	22
s6-5	5	-4	324	-5	335	17	13	-8	10	10	9	324	17
s6-7	6	-7	323	-8	336	18	12	-9	6	6	6	324	20
s7-2	10	-7	326	-8	336	15	13	-15	7	5	5	328	16
s7-4	10	-7	327	-5	336	16	11	-10	7	7	6	324	17
s7-6	9	-8	326	-6	337	11	13	-10	9	9	9	324	17
s8-2	6	-12	325	-3	336	10	14	-27	9	9	5	330	11
s8-4	6	-12	324	-7	335	13	13	-30	7	8	6	328	16
s8-6	7	-13	326	-8	337	11	15	-27	11	10	7	329	22
s11-2	11	-13	329	-10	338	17	14	-18	1	2	2	328	19
s11-4	8	-11	323	-6	335	17	13	-17	2	2	1	323	20
s11-6	7	-15	325	-8	336	12	13	-18	1	1	1	325	17
s15-2	9	-14	323	-8	335	23	19	-36	0	0	0	329	18
s15-3	14	-16	323	-5	336	26	19	-49	0	0	0	332	18
s15-5	12	-16	325	-2	337	20	20	-46	0	0	0	330	10

Table 3: Back to the Motion Runs (Counter Clockwise)

[Note: For Tables 2 and 3, the subscript numbers correspond to the following specific times:

- 1 - time of maximum SPV during acceleration
- 2 - 90 s
- 3 - 140 s
- 4 - 305 s
- 5 - time of horizontal SPV "reversal"
- 6 - time of maximum SPV during deceleration.]

Horizontal SPV. The horizontal SPV response during forward facing CW runs (Figure 2a) appears to be the mirror image of the backward facing CCW response (Figure 2c). Both CW and CCW runs show a transient "yaw response" at the start of centrifuge deceleration, where the SPV response proceeds in the same direction as during acceleration.

For six of the eight subjects, the mean horizontal SPV response during centrifuge acceleration was greater when the subject faced the motion (CW) as compared to when the subject had his back to the motion (CCW). One subject (s11) showed no difference in the mean response, and one subject (s15) had a slightly greater mean response (0.67 deg/s). Four of the eight subjects (s3, s5, s6 and s7) had significant greater yaw response when facing the motion (paired *t*-test applied individually by subject; $p < 0.05$).

Vertical SPV. An up-beating nystagmus was evident in seven of the eight subjects during the constant velocity phase of the centrifuge run. Because the stimulus to the vestibular system during the constant

velocity phase is a linear acceleration greater in magnitude than 1 G, we conclude that this response is an LVOR and use the term L_z nystagmus as defined by Young (9).

There was no apparent effect of run direction (CW vs. CCW) on the magnitude or direction of the sustained component of L_z nystagmus. This supports the linear acceleration origin of this response, since the linear stimulus has a +Z-axis direction for both forward and backward facing configurations even though the angular stimulus is reversed. To assess L_z nystagmus sensitivity, we measured the vertical SPV at time = 90 s (V_2 ; Figure 4). Subjects displayed a range of V_2 values across individual runs from -1 to 21 deg/s (Figure 4), and excluding responses from run 1, a range of mean V_2 values from 0 to 10 deg/s. Excluding subject s15, who had no significant L_z nystagmus, the average static L_z nystagmus sensitivity to vertical linear acceleration is 8 deg/s. Assuming a linear response to G, the average static L_z nystagmus sensitivity is approximately 3 deg/s/G.

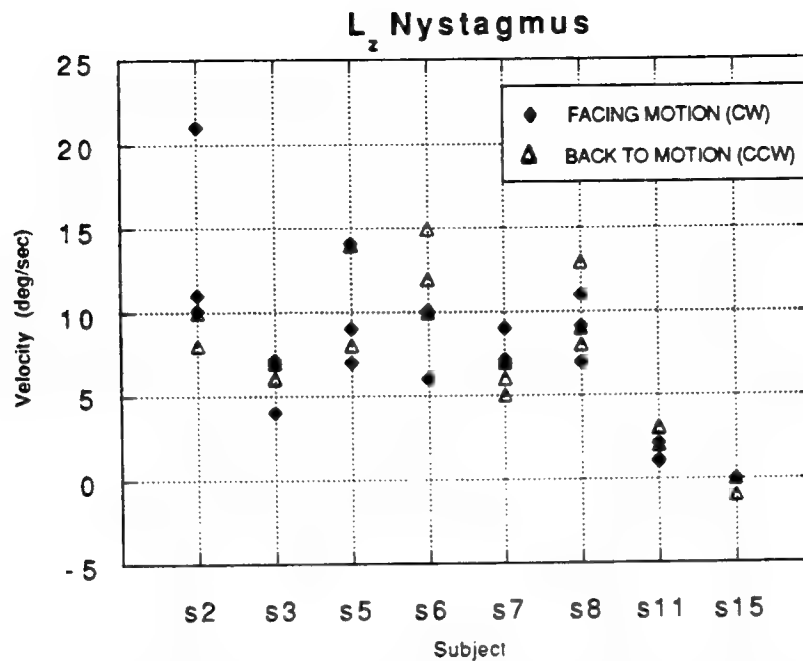


Figure 4. L_z nystagmus magnitude at 90 secs (V₂) for 8 subjects.

Analysis of variance (ANOVA, Systat 5.2) of the V₂, V₃, and V₄ data revealed significant effects for subject, (V₂: $F = 18.7$; V₃: $F = 20.3$; V₄: $F = 35.6$; $p < 0.001$) but not for run direction. Dropping each subject's first run for reasons discussed earlier, intersubject differences in V₂, V₃, and V₄ remained significant (V₂: $F = 24.3$; V₃: $F = 29.5$; V₄: $F = 26.7$; $p < 0.001$).

Figure 5 shows the geometric means for the ratios of peak vertical SPV during centrifuge deceleration versus acceleration for CW and CCW runs. We calculated the following ratio to determine if there was a significant difference between the vertical SPV response during acceleration and deceleration, that corresponded to the observed asymmetry in pitch sensations.

$$\text{Ratio (dec/acc)} = \left| \frac{V_6}{V_1} \right|$$

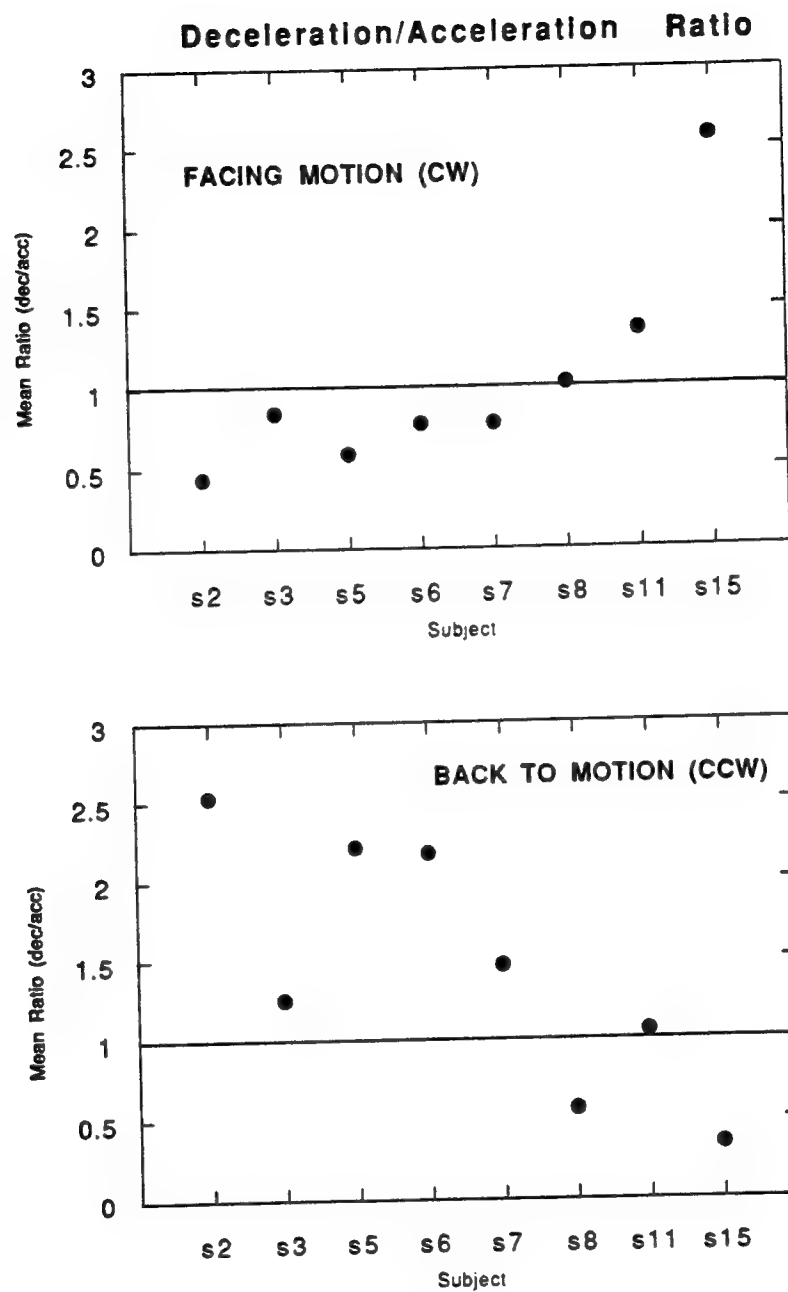


Figure 5. Geometric means for the ratio of centrifuge deceleration versus acceleration peak vertical SPV. Facing motion (CW) and back to the motion (CCW).

Discussion

Our results are consistent with the view that the total human VOR response to centrifugation is composed of interacting angular and linear VOR responses. The total vertical VOR response did not follow the predicted model response exactly (Figure 3), since it appears that a linear VOR interacts with the angular VOR during the period of the angular VOR response. Evidence of this interaction can be seen when comparing the time constant of vertical SPV onset during centrifuge acceleration for the two directions. During acceleration, the L_z nystagmus interacts with the angular nystagmus, decreasing the magnitude and time of peak vertical SPV response for back to the motion CCW runs (-20 deg/s at 13 s) as compared to facing the motion CW runs (34 deg/s at 18 s). Further evidence that the L_z nystagmus has modified the angular VOR comes from subject s15's data. This subject had no steady state L_z nystagmus, and his mean time of peak vertical SPV when facing the motion, 18 s, was almost the same mean time when his back was to the motion, 19 s. The build up and decay of L_z nystagmus occurs at the same time as the angular VOR. Therefore the exact dynamics of the L_z nystagmus and the dynamics of the cross-coupled angular VOR are difficult to determine separately.

An interesting result is obtained by comparing the experimental data with the model data (Figure 3). There was not a good qualitative correlation between the experimental SPV response and the predicted velocity storage model SPV response, especially for the vertical or pitch plane response. The velocity storage model uses parameters that were calculated from velocity storage experiments conducted in 1 G. Since central angular velocity storage mechanisms are G dependent (7), these parameters may not be appropriate for this experiment. Therefore, model predictions from a "cupula only" model were added to Figure 3. This cupula model response provides a qualitatively

better fit to the experimental data than the velocity storage model response. This suggests that there may be a reduced influence of central angular velocity storage mechanisms in the total VOR response in 3 G_z as compared to 1 G_z environments. Further research is needed to investigate the role of central velocity storage mechanisms in hypergravity environments.

If peak vertical SPV magnitudes were a predictor of the reported pitch sensation asymmetry, then we would expect that the deceleration/acceleration ratios shown in Figure 6 would be greater than 1 for both directions. This is not the case. For facing the motion runs, the subjects that showed a L_z nystagmus had a ratio less than 1. This result was expected because the up-beating L_z nystagmus adds to the acceleration response and subtracts from the deceleration response. Conversely, for back to the motion runs, the ratio of deceleration/acceleration is greater than 1 for subjects who showed an L_z nystagmus except Subject s8. Subject s11 showed little L_z nystagmus and the deceleration/acceleration ratio is greater than 1 for facing the motion runs, and approximately 1 for back to the motion runs. Subject s15, who had virtually no steady state L_z nystagmus, showed an asymmetric response in pitch. For this subject, the pitch down response was consistently greater than pitch up response. Whether this is simply intrinsic to the subject's oculomotor system such that it would also be manifest in VOR responses to rotation about the earth vertical, or whether it involves interactions between angular responses and gravito-inertial force is unknown. At any rate, the peak vertical SPV magnitude does not correlate with reported pitch sensations. For a complicated stimulus such as that used in this experiment, the combination of semicircular canal cues, otolith cues, proprioceptors, and tactile cues apparently combine to give perceptual sensations that are not reflected in simple measures of the vestibular response, such as the magnitude of peak SPV.

The observed L_z nystagmus in 7 of the 8 subjects provides further evidence that a vertical LVOR can be elicited by a constant vertical linear acceleration (11, 12, 21). The LVOR response likely originates in the otolith organs. Repeat testing showed that the L_z nystagmus response was a consistent individual subject characteristic. Seven subjects displayed an L_z nystagmus response, whereas one subject had no L_z nystagmus. The magnitude of the L_z nystagmus in two subjects decayed substantially over the 5 min run, whereas the magnitude of the L_z nystagmus remained essentially constant in the other five subjects over the 5 min run.

Young (9) estimated an L-nystagmus in the head vertical direction of 4 deg/s/G, and in the horizontal direction, a sensitivity of 9.7 deg/s/G. He hypothesized that L nystagmus is caused by utricular shear, and argued that with the head upright, the vertical sensitivity should be lower than the horizontal since the utricles are tilted 30 deg up from the horizontal plane. Marcus and Van Holten (12) observed an average vertical L_z nystagmus sensitivity of 9 deg/s/G. In our experiment, the average static L_z nystagmus sensitivity was approximately 3 deg/s/G. This value is lower than the 4 deg/s/G estimated by Young, and lower than the value estimated by Marcus and Van Holten. Other than L_z nystagmus magnitude differences, our results are consistent with those of Marcus and Van Holten, and the magnitude differences are possibly attributable to our use of ISCAN, which avoids artifacts in measuring vertical eye velocity.

Previously, L_z nystagmus has usually been observed during changing magnitude linear acceleration, but the L_z nystagmus in the present centrifuge runs occurred in response to a steady state linear acceleration. Merfeld (22) observed an LVOR response when there was a difference between the direction of the resultant gravito inertial force and the direction of gravity. To account for this response, Merfeld hypothesized "that

gravito-inertial force is resolved into two components; one representing an internal estimate of linear acceleration and one representing an internal estimate of gravity." Extending this hypothesis to the case when there is a difference between the magnitudes of the resultant gravito-inertial force and gravity, we propose the following explanation for the observed L_z nystagmus. When subjected to a constant 3 G_z gravito-inertial force, the otolith organs send a signal to the central nervous system that is resolved into two components. These are a 1 G gravitational field aligned with the body Z axis and an upward linear acceleration of magnitude 2 G . The functionally appropriate response is the observed up-beating L_z nystagmus.

In our preliminary runs, EOG recordings indicated exceptionally strong L_z nystagmus in one subject during a 3 G run. None of the eight military aviator candidates analyzed in this experiment showed an exceptionally large L_z nystagmus. The L_z nystagmus in our sample did not appear to be of sufficient magnitude to override visual oculomotor control, however, L_z nystagmus was idiosyncratic. Studies are continuing to determine if some individuals have a large L_z nystagmus sensitivity and to estimate the range of this potentially debilitating response. Further visual studies are required to determine the magnitude of the L_z nystagmus that would blur vision during high G maneuvers.

The "yaw response" at the start of centrifuge deceleration observed in both facing the motion and back to the motion runs (Figures 2a and c), is predicted by the mathematical model for the human angular VOR (Figure 1). This brief horizontal transient is attributable to the cross-coupled components of the total horizontal canal stimulus being initially greater than, and opposite in direction to, the component arising from the angular deceleration of the centrifuge. The yaw angular acceleration stimulus during centrifuge acceleration and deceleration changes sign due to the pendulous chair swinging through 70.5 deg (23). During

centrifuge acceleration, this sign change in the yaw angular acceleration stimulus is not of sufficient strength to change the sign of the yaw angular velocity, however it reduces the time of peak SPV. During centrifuge deceleration, the sign change in yaw angular acceleration produces a reversal in yaw angular velocity. The yaw reversal during centrifuge deceleration can be seen in the model and the SPV response.

In six subjects, the mean horizontal peak SPV magnitude during centrifuge acceleration was greater when the subject faced the motion (CW) as compared to when the subject had his back to the motion (CCW). Four of the subjects had significant differences. This result suggests that a horizontal linear force was present during acceleration of the centrifuge, causing a horizontal LVOR to modify the total horizontal VOR response (22). When the subject was facing the motion, the angular VOR and the LVOR are additive, and when the subject had his back to the motion, the angular VOR and the LVOR subtract. Therefore, the mean horizontal peak SPV magnitude during centrifuge acceleration would be greater when the subject faced the motion as compared to when the subject had his back to the motion. The two subjects (s11 and s15) who did not show a horizontal SPV difference when facing the motion versus back to the motion also had weak or no vertical L_z nystagmus during constant centrifuge velocity; the VOR of these subjects may be unresponsive to linear acceleration.

In summary, when a subject is exposed to combined linear and angular accelerations during centrifuge acceleration and deceleration, the total VOR response is composed of interacting angular and linear VOR responses. The observed VOR response qualitatively follows the predictive model well, however, large differences in spatial orientation perception between centrifuge acceleration and deceleration are not seen in the total VOR response. Thus spatial orientation perceptual responses can not be inferred from the VOR response when

subjected to a complex vestibular stimulus. Large differences in spatial orientation perception are present when the centrifuge angular acceleration and deceleration magnitudes were low.

During the constant hyper-G phase of the centrifuge run, a sustained up-beating (" L_z ") nystagmus was observed in 14 of 15 subjects. This observed L_z nystagmus provides further evidence that a vertical linear VOR can be elicited by a constant vertical linear acceleration. Repeat testing showed substantial individual differences in L_z nystagmus magnitude, and such differences were maintained over the several test sessions. Using a eye movement recording method that avoided artefacts in the vertical direction, the average static L_z nystagmus sensitivity was approximately 3 deg/s/G. The magnitudes of the L_z nystagmus in our subject sample did not appear sufficient to degrade visual acuity, however further research is required to determine the magnitude of the L_z nystagmus that would cause vision problems during high G maneuvers.

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Other NAMRL Publications

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